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REVIEW

Browning events in Arctic ecosystems: Diverse causes with common consequences

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Abstract

Arctic ecosystems are experiencing extreme climatic, biotic and physical disturbance events that can cause substantial loss of plant biomass and productivity, sometimes at scales of >1000 km^2. Collectively known as browning events, these are key contributors to the spatial and temporal complexity of Arctic greening and vegetation dynamics. If we are to properly understand the future of Arctic terrestrial ecosystems, their productivity, and their feedbacks to climate, understanding browning events is essential. Here we bring together understanding of browning events in Arctic ecosystems to compare their impacts and rates of recovery, and likely future changes in frequency and distribution. We also seek commonalities in impacts across these contrasting event types. We find that while browning events can cause high levels of plant damage (up to 100% mortality), ecosystems have substantial capacity for recovery, with biomass largely re-established within five years for many events. We also find that despite the substantial loss of leaf area of dominant species, compensatory mechanisms such as increased productivity of undamaged subordinate species lessen the impacts on carbon sequestration. These commonalities hold true for most climatic and biotic events, but less so for physical events such as fire and abrupt permafrost thaw, due to the greater removal of vegetation.

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Counterintuitively, some events also provide conditions for greater productivity (greening) in the longer-term, particularly where the disturbance exposes ground for plant colonisation. Finally, we find that projected changes in the causes of browning events currently suggest many types of events will become more frequent, with events of tundra fire and abrupt permafrost thaw expected to be the greatest contributors to future browning due to their severe impacts and occurrence in many Arctic regions. Overall, browning events will have increasingly important consequences for ecosystem structure and function, and for feedback to climate.

Introduction

In recent years, Arctic ecosystems have been increasingly exposed to a range of extreme disturbance events that can cause acute and extensive loss of plant biomass at tens-of-meters to landscape and greater scales [1–3]. These abrupt losses of biomass are termed "browning events", and contribute to the broader phenomenon of reduced biomass and productivity known as "Arctic browning" [4,5] which is an important driver of tundra vegetation dynamics and of complexity within the more widespread Arctic "greening" trend [6–9]. Browning events in Arctic ecosystems are caused by numerous and diverse disturbances, including climatic (such as extreme winter warming, frost drought, and icing), biological (such as invertebrate and vertebrate herbivore outbreaks, and pathogens) and physical disturbances (such as fire, or abrupt thermal erosion from permafrost thaw). The resulting browning is important because of the large magnitude of damage and the consequences for ecosystem structure and function, including loss of biomass, changes in biodiversity and vegetation dynamics, and feedback to climate through altered carbon (C) and energy balance [2,10,11]. The consequences of some browning events for local people and their livelihoods can also be significant [12]. It is therefore of concern that most types of disturbances that cause browning are expected to become more frequent, largely due to the direct or indirect influences of climate change [3,13–15]. Because of the often-substantial impact and increasing importance of browning events, it is now timely to synthesise current understanding of these diverse phenomena [7,8].

Within the press-pulse framework [16], the acute events that cause the browning are classed as "pulse" disturbances. They are also often referred to as "extreme events", especially when referring to climatic extremes [17]. These pulse disturbances contrast with "press" disturbances that occur gradually over a longer duration, so within this framework it is the gradual 'press' of climate change that make the pulse disturbances that cause browning to be more frequent and/or intense [16]. Ecologists recognise that pulse disturbances (extreme events) are of major importance across ecosystems globally, with substantial impacts that are often disproportionate to their short duration, including increased probability of pushing organisms past lethal thresholds [17,18]. Recent research recognises this importance across high latitude ecosystems including the Arctic and the Antarctic [7,19–21], the boreal biome and alpine ecosystems [7,22].

For ground-based ecosystem responses that are the focus of this review, we define the browning events that result from the pulse disturbances as "significant declines in biomass, productivity, or *in situ* indices of these (such as Normalized Difference Vegetation Index (NDVI)) that occur within a year". Browning events also have a definition in remote sensing, being referred to as "spectral browning events that are short-term decreases in vegetation indices" [6]. We focus on the ground-based definition given our aim to review the ecosystem responses that occur.

At the scale of the individual browning event, the capacity for significant disruption of productivity and vegetation dynamics has been documented in clear examples. For instance, in 2007 the Anaktuvuk River fire in Alaska burned more than 1000 km^2 of tundra and the resulting release of C was of similar magnitude to the annual net C sink for the entire Arctic tundra biome [23]. A single Extreme Winter Warming event in Northern Scandinavia (2007) caused widespread plant mortality resulting in a 26% reduction in NDVI over more than 1400 km^2 [24]. However, despite the capacity for substantial impacts, the spatial and temporally discrete nature of browning events means they are unlikely to be fully apparent in long-term trends of satellite data [8], and therefore connecting browning events on the ground to the temporal and spatial dynamics in pan-arctic greenness remains challenging [6]. Part of the challenge is that the level of understanding among different types of browning events varies greatly, and the magnitude, spatial distribution and scale of some event types is either poorly understood or not known, so their contribution to the larger scale patterns of Arctic browning and greenness dynamics remain unclear. This also causes problems for incorporating browning events into models and projections. None-the-less, should the influence of browning events over Arctic ecosystems continue to increase, adjustments will be needed to models that may otherwise overestimate the increase in Arctic biomass with climate change, and therefore the consequences for C sequestration and climate feedbacks [25,26]. So, while modelling and remote sensing approaches provide the necessary tools for upscaling impacts and making future predictions, on-the-ground ecological understanding (the focus of this review) is needed to characterise the mechanisms causing browning for inclusion in modelling efforts and to robustly capture their impacts across the Arctic.

Given the increasing importance of, and research on, Arctic browning events, our review aims to (i) synthesise understanding of browning events and their underlying pulse disturbance drivers; (ii) identify impacts on biomass and C dynamics; (iii) compare commonalities and key contrasts between browning events to provide a broad-based understanding of browning on the ground; and (iv) highlight research gaps and knowledge needs, considering the varying levels of understanding of the different types of browning events. Our review synthesizes observational and experimental studies of browning events in Arctic and sub-Arctic tundra ecosystems. We do not cover high latitude forest ecosystems [7,27,28], but we do include tundra-type vegetation (i.e., functionally and compositionally 'tundra') when it is the dominant vegetation community within sparse sub-Arctic woodlands. Because of the large diversity of different Arctic browning events, we do not provide an exhaustive review of all known effects of each, but instead focus on their key features and attributes, and the responses most widely assessed (including plant mortality, productivity and C cycling) that then allow us to draw out commonalities and key contrasts.

Arctic browning events: causes, characteristics and future change

Climatic events: winter is more important than summer

Extreme winter warming. Extreme winter warming events see temperatures increase abruptly to above freezing, melting snow and exposing vegetation to unseasonably warm temperatures. This can induce "spring-like" bud-burst in mid-winter, resulting in loss of frost tolerance (Fig 1A), and therefore high rates of shoot mortality upon the return of ambient winter cold [24,29,30]. Extreme winter warming events have previously been uncommon, though data suggest increases since the 1950s in Scandinavia and parts of Alaska [15]. With the Arctic warming potentially four-times faster than the rest of the globe [31], an increase in frequency of extreme winter warming events is expected [32] (Table 1), and analyses project that winter warm spells will double or triple in frequency by 2100 in Scandinavia [14,33]

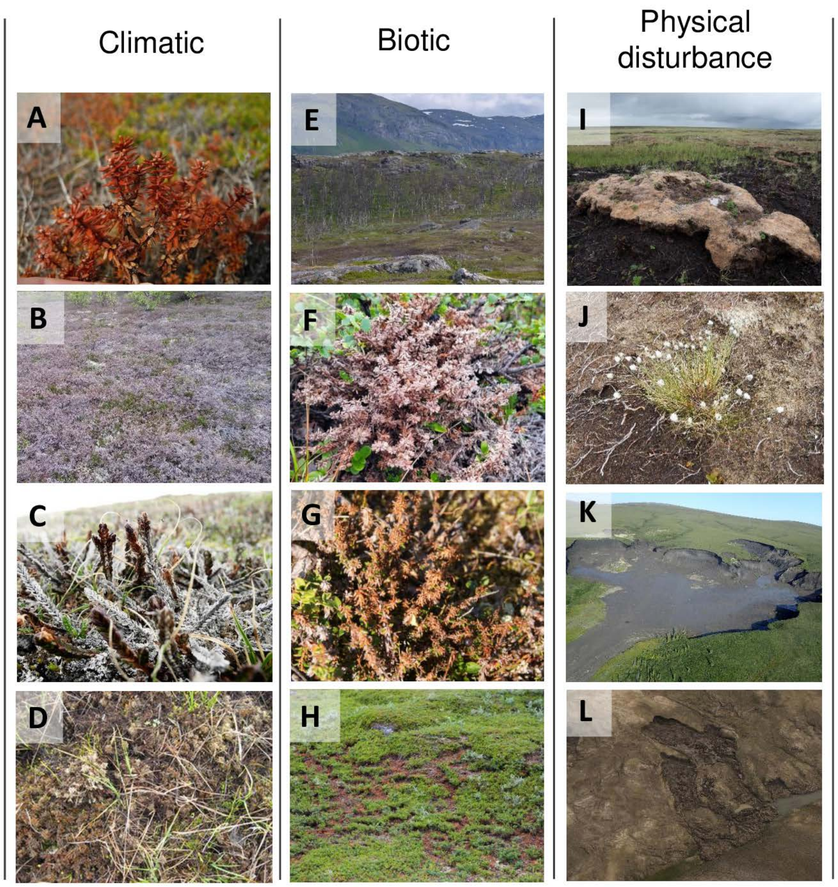

Fig 1. Examples of browning events arising from climatic, biotic and physical disturbance events. (A) *Empetrum nigrum* shoot mortality following an extreme winter warming event in northern Norway. (B) Almost 100% mortality from frost-drought of the dominant dwarf shrub *Calluna vulgaris*, Norway. (C) Dead *Cassiope tetragona* following an icing event, Svalbard, High Arctic. (D) Droughted *Sphagnum* from a combined heat-wave drought, Utqiaġvik, Alaska. (E) Spread of an *Epirrita autumnata* caterpillar outbreak at treeline from birch woodland onto tundra. Grey vegetation in foreground is defoliated *Betula nana* (dwarf birch) shrubs, grey trees mid-picture are defoliated tree birch (*B. pubescens* spp. *czerepanovii*) that is the source of the outbreak (sub-arctic Sweden). (F) Dead shoots of *E. nigrum* infected with the snow mould *Arwidssonia empetri*. (G) Dead *E. nigrum* following a caterpillar outbreak of *E. autumnata* and *Operophtera brumata*. (H) Browning from lemming grazing. (I) Aftermath of fire in the Yukon-Kuskokwim delta, Alaska, showing a dead *Sphagnum* mound and significant removal of the peaty organic layer. Abundant resprouting of *Eriophorum vaginatum* (cotton grass) clearly visible in mid-ground. (J) Resprouting of *E. vaginatum* a year after fire. This heathland was fire-prone due to a previous frost-drought event that left dead, dry, flammable vegetation. (K) A large retrogressive thaw slump (a megaslump >20 ha), Peel Plateau, NW Canada. (L) Active layer detachments near Eureka, Ellesmere Island. Photos: (A, C, G) Rachael Treharne (B, J) Gareth Phoenix (D) Donatella Zona (E) Thomas Parker (F, H) Johan Olofsson (I) Chris Linder (K) Julian Murton (L) Antoni Lewkowicz.

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(Table 1). However, while there is clear evidence of browning resulting from extreme winter warming (e.g., [24,34]), uncertainty in the climatic thresholds that need to be exceeded to cause plant damage (especially the temperatures and duration needed to induce premature bud burst) places great uncertainty in predicting browning from their extreme winter warming driver.

Table 1. Characteristics of browning events. Durations and reported ranges of % damage from real events, not field simulations. 'nd' indicates no data. Superscript letters refer to notes as follows: (a) based on recovery of biomass or cover; (b) note, total area of impact often not reported in surveys of amount of damage, (c) not quantified but based on similarity of impact compared to extreme winter warming; (d) combined drought and heatwave; (e) at small scales scorching can result in little biomass removal, though fire typically burns >70% vegetation cover; (f) a thermal erosion feature often continues to expand, so duration only refers to a single point; (g) area includes thermokarst lake and wetland development; (h) beaver dams listed separately since the browning mechanism is dam creation, not herbivory of biomass; (i) decades to centuries for complete biomass recovery. Nordic Arctic region here refers to Norway (including Svalbard for icing events), Sweden and Finland north of the Arctic Circle.

Browning Event	Duration of browning[a]	% loss of biomass or live shoots[b]	Where currently observed?	Recent or projected change in causes	Pan-arctic outlook
Climatic Events					
Extreme winter warming	2–4 yrs [128]	23%–95% [29,34]	Nordic Arctic region [2,24,35]	2x to 3x increase in frequency of extreme winter warming by 2100 (Northern Fennoscandia, Svalbard and Jan Mayen) [14]. Arctic warm spells in winter are increasing [33]. In regions of lower and/or declining snowfall, extreme winter warming will need less warmth to expose vegetation.	Increases Scandinavia and parts of Alaska since 1950s [15]. Positive trend in the number of winter warming events in western and eastern Greenland (1979–2013) [162]. However, linking changes in climatic events to changes in browning events is challenging.
Frost-drought	2–4 yrs (c)	42%–60% [2,36]	Nordic Arctic region [34,36].	Areas projected to receive less snow may see increased frequency [163,164].	No knowledge of global distribution of browning events, though less snow (and hence increased risk) projected for European and western American Arctic [163,164]. Linking those changes to changes in browning is challenging.
Icing	nd	10–50% [34,35]	Browning observed in Nordic Arctic region, though icing and rain-on-snow distributed widely in Arctic coastal climates [42].	No significant increase in Arctic-average Rain-on-Snow frequency (1979–2009) but high regional variability [49,160] suggests regional increases in browning from icing possible. Increase possible due to warmer winters and more winter precipitation falling as rain [12,52].	Areas with the largest simulated positive RoS trends are typically located over regions with higher snow accumulation in coastal climates, such as Scandinavia, Baffin Island, Alaska and Kamchatka [163]. Linking these changes to browning is challenging.
Summer frost	nd	nd	Norway [2]. Browning events not widely reported.	May decrease due to fewer cold spells [33,62] and warmer summer minimas [165].	Less likely in most Arctic regions due to projected ongoing summer warming.
Summer heatwave	1–2 yrs [61](d)	20% [61](d)	Utqiagvik, Alaska [61](d) Browning events not widely reported.	May increase due to more extreme warm spells in the Arctic [33,62,165,166].	All areas of Arctic projected to experience summer warming so browning may become more common, but uncertainty in linking heatwaves to browning makes predictions challenging.
Summer drought	1–2 yrs [61](d)	20% [61](d)	Utqiagvik, Alaska [61](d). Browning events Not widely reported.	May increase due to greater evaporative demand, more heatwaves driving more drought [62], or due to early snowmelt or permafrost thaw reducing soil moisture [167,168]. May decrease due to greater annual, spring and summer rainfall [52].	Changes in soil moisture projected for high latitudes [169] but unclear the extent this will lead to drought induced browning events.
Physical Disturbance Events					
Fire	2–10 yrs, vascular plant. >25 yrs, moss/lichens [10,65,110,133]	61(e)–100% [10,23,65,110]	Pan-Arctic distribution (more in Alaska and north-Eastern Siberia) [13]	Frequency in Alaska will more than double by end of century [69]. Increase due to warming and drying, greater fuel load and frequency of lightning strikes [13,69]. Decrease due to greater summer precipitation [13].	Fire widely distributed. Frequency moderately correlated with sea ice extent, so ongoing sea ice melt suggests ongoing increase in browning from tundra fire, and more lighting strikes and greater fuel load will also contribute [13,170,171]
Extreme permafrost thaw events	~10–20+ yrs [137](f), [117]	20%–100% [117,84,121]	Pan-Arctic in ice-rich permafrost zones.	Increasing. Area of abrupt permafrost thaw (g), 0.9 million km^2 in 1900, 1.6 million km^2 in 2100 under RCP 8.5. Specifically for slumps, detachments and gullies ~70,000 km^2 by 2100 [11]. Increases likely due to warming and more summer precipitation [52,11,86].	Given pan-Arctic warming: ice-rich permafrost regions, especially on hillslopes, beside rivers or coastal at risk of increases [11,87] leading to more associated browning.

(Continued)

Table 1. (Continued)

Browning Event	Duration of browning[a]	% loss of biomass or live shoots[b]	Where currently observed?	Recent or projected change in causes	Pan-arctic outlook
Biotic Events					
Herbivore outbreaks	1–2 yrs [91,121,125]	12%–48% [34,92,99,121,124,125]	Pan-Arctic though strong focus on evidence from Scandinavia and Greenland [100].	Defoliating caterpillars of sub-Arctic woodland have recently started to occur in low Arctic tundra [98]. The spread and greater frequency of outbreak in sub-Arctic woodland [90], suggests increasing outbreaks could occur on tundra. In contrast, poorer snow conditions for lemmings arising from warming may reduce population outbreaks [95].	Unclear, though regional evidence would suggest defoliating invertebrates such as moth caterpillars will spread [90], while ongoing warming may continue to reduce the quality of snow conditions for lemmings [95].
Beaver dams [(h)]	Centuries [(i)], [104]	100%	Alaska, Canada - not Canadian archipelago [101,102].	Considerable increases this century. Location specific case studies suggest increase in activity of 2–50 fold [101,102].	Given improved habitat for beaver (e.g., unfrozen water, more and taller shrubs) are climate change driven, a continued increasing trend across the American Arctic looks likely, facilitated by reduced hunting pressure [101]. Eurasian beaver not reported in tundra yet.
Pathogens	2 yrs [106]	70% [106]	Sweden	No estimates of current or future frequency or distribution. Snow moulds may increase in areas where snow persists longer [106], though overall, the Arctic is experiencing declining snow cover [172]	Given the decline in snow cover broadly for the Arctic [172], snow mould browning events may become less common.

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Frost drought. Frost drought occurs when exposure of shoots above the protective snow layer promotes transpiration, while frozen soils simultaneously prevent water uptake (Fig 1B) [2,35,36]. Frost drought events are more likely with warmer winter air temperatures and sunny and windy days that stimulate stomatal opening and increase leaf transpiration [2,37]. Evergreen species are more susceptible than deciduous species due to winter foliage allowing transpiration [2,34,36]. Reductions in snow cover, depth or area, and increasing frequency of winter warm periods [14] suggest frost drought may become increasingly important (Table 1). However, uncertainties on the links between climatic conditions of frost drought events and the occurrence and magnitude of plant damage means that current modelling is limited to the site level, with pan-Arctic analyses and future projections still in development [38].

Icing events. Icing can be caused by rain-on-snow, where winter rainfall and melted snow refreezes around vegetation [35,39], or by winter warming that (partially) melts the snow pack, followed by re-freezing. Ice encasement can result in plant damage or mortality [40,41] (Fig 1C, Table 1). Rain-on-snow events appear more typical of maritime Arctic regions, including parts of Alaska, the Canadian Archipelago, Greenland, Scandinavia, Svalbard, and Kamchatka [15,35,42] (Table 1). The mechanisms of damage from icing events remain uncertain, though probably arise from either one or a combination of: (i) exposure to extreme cold due to the loss of insulating snow and poor insulating properties of ice, (ii) hypoxia and/or toxicity from CO_2 accumulation due to the impermeability of the encasing ice, or (iii) mechanical damage. However, none of these offer satisfactory explanations since Arctic vascular plants are often tolerant of experimental ice encasement [40,43,44], and of experimentally imposed hypoxia and high CO_2 [45]. Lichens show both damage from, and protection by, icing [46,47], and it has been suggested that greater tolerance will occur where any (prior) warming associated with the icing event does not initiate physiological activity [41].

Evidence suggests an increase in the frequency of the drivers of icing, including rain-on-snow and freezing rain [48–51], more winter precipitation falling as rain rather than snow [52] and more ice layers in snow [53] (Table 1), but projecting this to future vegetation browning is yet to be done.

Climatic events during the growing season: drought and heatwaves. Growing season drought can reduce growth of tundra plants [54,55] and ecosystem productivity [56–59], and experimental heat waves have led to leaf mortality and senescence [60]. However, there is less evidence to suggest that summer drought events are an important component of event-driven browning (i.e., substantial mortality arising from an extreme and acute drought). While currently rare, combined drought and heat waves can cause browning as seen in 2007 at Utqiaġvik, Alaska [61], where the driest and fifth warmest summer in 65 years caused severe desiccation (and hence browning) of *Sphagnum* in wet sedge tundra (Fig 1D; Table 1). Analyses suggest heatwaves may have increased the most for tundra in parts of Greenland, mainland Canada and the Chukchi sea region [15]. Increasing importance in the future is indicated by recent trends toward more daily warm temperature extremes [32,62], and a pan-Arctic analysis showing more frequent warm spells in summer [33]. However, an increase in drought events currently remains uncertain due to a lack of comprehensive assessment over the terrestrial Arctic [32], and since greater spring and summer rainfall and annual precipitation are projected for most Arctic regions (Table 1) [52,63].

Climatic events during the growing season: frosts. Growing season damage from frost is most likely to occur when new growth coincides with cooler temperatures in spring [41,64]. However, increases in these since the 1950s seem largely limited to Norway and west Greenland [15] and browning events from this have very rarely been observed [2] (Table 1).

Overall, currently it appears that winter climatic events are more important to Arctic browning than growing season climatic events.

Physical disturbance events: the most widespread and severe browning events

Fire. Fire combusts vegetation and surface organic soil layers, with the extent of combustion increasing with burn severity [65,66] (Fig 1I & Fig 1J, Table 1). Fires occur throughout the Arctic tundra biome, though currently greatest fire frequencies are in Alaska and northeastern Siberia (~200km^2 yr^{-1} and ~6000km^2 yr^{-1} respectively) [67,68]. Fire occurrence is positively related to summer temperatures and ground aridity, and negatively related to summer precipitation [13,69–70] (Table 1). Lightning ignitions also explain a large part of the burned area in boreal forests and may play a similar role in tundra [71–73]. However, biome-wide understanding of fire regimes is a challenge because global satellite data products generally underestimate burned area [74,75]. Nonetheless, regional burned area products derived from remote sensing data reveal a step increase in fire frequency in Alaskan tundra beginning in 2010 [76], and substantial increases in area burned in Siberian tundra during the extreme 2019 and 2020 fire seasons [68].

Across the tundra biome, fire is more likely to occur in erect-shrub tundra and graminoid dominated tussock tundra than other tundra vegetation types [67,77]. Consequently, larger fuel loads associated with ongoing expansion of large stature shrubs ("shrubification" [78]) and more general biome-wide productivity increases may contribute to increased fire frequency [71,79]. Therefore, the predicted changes in temperature, convective air mass flux and lightning frequency could cause an increase in lightning-ignited fires [80]. Indeed, it is estimated that the rate of burning in Alaskan tundra will approximately double by the end of this century [13]. Fire may become one of the most rapidly increasing event drivers of Arctic browning (Table 1).

Abrupt permafrost thaw. Abrupt permafrost thaw includes retrogressive thaw slumps, active layer detachments, thermo-erosion gullies [81], sinkholes, and thermokarst lake and wetland development [11,82]: within our definition of a browning event, we focus on active layer detachment slides (Fig 1L) and retrogressive thaw slumps (Fig 1K). We acknowledge though that other thaw processes can potentially be described as 'abrupt' [11,83]. Note also that for retrogressive thaw slumps, the initial browning is an abrupt event, and further browning then occurs as the slump expands.

In active layer detachments, seasonally thawed topsoil detaches from the permafrost underneath, leading to sudden mass wasting that either removes the vegetation or creates moving islands of displaced vegetation [84–86] (Fig 1). In retrogressive thaw slumps, a thawing headwall collapses, exposing more permafrost to thaw and collapse, and this process repeats so that the headwall retreats into the landscape (Fig 1). Headwalls retreat at a mean rate of 6.5 m yr^{-1} [11], though rates vary greatly from as little as one m yr^{-1} to tens of metres per year up to maxima outliers of ~70 m yr^{-1} [86,87]. While a single event does not have the considerable spatial extent seen for fires or climatic and biotic events (Table 1), over longer timescales, thaw features can develop to cover large areas (e.g., the largest thaw slump, the Batagay megaslump in NE Siberia, now covers >1 km^2), and the cumulative impact of a large number of these events with pan-Arctic distribution will be substantial (Table 1). For instance, the area undergoing active slumping, detachments, and gully formations may exceed 60,000 km^2 by 2100 (under RCP 8.5) (this figure includes boreal as well as Arctic permafrost) [11].

Biotic events: increasing impacts and new areas affected

Vertebrate and invertebrate herbivores. Although large herbivores such as reindeer/caribou and muskoxen experience strong population cycles and have dramatic effects on vegetation [88,89], these cycles are in most cases too gradual to cause rapid declines in vegetation that would fall under our definition of a browning event. However, voles, lemmings and herbivorous insects are present in most vegetated areas in the Arctic [90,91], and lemmings especially are well known for the reduction in plant biomass caused by their dramatic population peaks [92,93] (Fig 1H, Table 1). Decline in lemming populations have been linked to warmer weather during snow onset though the cyclic dynamics of lemming populations do not currently appear threatened [94]. None-the-less, well documented herbivory-driven, landscape-scale browning events have been observed [92], but further research is needed to characterize the extent of their occurrence, as well as to assess how declining winter snow conditions may modify outbreak frequency by reducing rodent populations [95] (Table 1).

Outbreaks of herbivorous insects also cause browning. The most studied species are the geometrid moths *Epirrita autumnata* and *Operophtera brumata*, whose caterpillar outbreaks defoliate the sub-Arctic birch forest at approximately decadal intervals (Fig 1E & Fig 1G), often spreading from the birch forest into the tundra [96,97]. Adding to concern, *O. brumata* is now reported to be developing and breaking out in tundra independent of a forest source [98] (Table 1). Outbreaks of the caterpillars of a noctuid moth, *Eurois occulta*, are also occurring regularly in Greenland [99]. However, outbreaks of canopy feeding caterpillars are not reported in all tundra regions [100], hence the pan-Arctic variation in the importance of browning events caused by geometrid moths needs further investigation.

In the past two decades, evidence shows increasing beaver (*Castor canadensis*) colonisation in the North American Low Arctic, [101,102] (Table 1), with this being recolonization following population lows from hunting. For instance, a 100 km^2 study region showed an increase in the number of dams from two to 98 between 2002 and 2019 [103] and beaver colonization doubled in areas of western Alaskan tundra between 2003 and 2017 [102]. Beaver dams can last more than 150 years, and the resulting flooding means that beaver dam numbers closely correlate with surface water area [104]. The abrupt removal of vegetation due to inundation, combined with wood-cutting by beaver (in both cases a removal of greenness), constitutes a browning event. One case study found beaver-influenced waterbody increases to be the majority (66%) of *all* waterbody increases [103], and so demonstrating the ability of beavers to drive localised browning in Alaskan tundra [102]. None-the-less, the importance at larger scales remains unclear. Furthermore, while the immediate impact of beaver activity is to reduce greenness, the longer-term consequence may be to increase greenness due to exposure of mineral substrate and water availability that may facilitate shrub expansion [101].

Pathogens. Snow moulds are fungi that infect evergreens and graminoids in a circumpolar range [105], but since many of the fungi-plant associations are species-specific, these outbreaks are only registered as browning events if their host plant is locally dominant. The best documented of these in the Arctic is *Arwidssonia empetri* attacking the evergreen dwarf shrub *Empetrum nigrum* (Fig 1F). *Arwidssonia* primarily infests plants by mycelia growing under the snow. Since mycelial growth is favoured by warm and wet conditions, infestations are more common in snow-rich years when the snow melts later in the season [106]. Although this phenomenon has only been studied in Scandinavia (Table 1), the distribution of the plant species and the fungal disease is circumpolar, so the same events may be expected throughout tundra regions. Again though, more research is needed.

Impacts on biomass and carbon fluxes: compensatory mechanisms can reduce impacts on net ecosystem exchange

Climatic events. A high level of shoot mortality is a common feature of browning events. Studies of extreme winter warming, frost drought, and icing report 10-80% shoot mortality (Table 1), with maximas of 80%, 60% and 50% reported respectively [2,24,29,35,36]. Research on non-vascular plants and lichens suggests these have greater tolerance than vascular plants. Lichens tolerate winter warming events because they can switch rapidly between states of metabolic rest and activity, and the poikilohydric nature of lichens and bryophytes can make them tolerant to desiccation and so tolerant of frost drought [107]. Bryophytes can, nonetheless, show physiological damage though not shoot mortality [108], and milder late-winters and springs could increase susceptibility to frosts [109]. Lichens can also show some sensitivity with prolonged ice encasement taking lichens beyond tolerance limits [47], though protection of lichens by ice cover has also been observed [46].

In terms of impacts on C fluxes, winter browning events result in the loss of photosynthetic leaf area and reduce C capture by the damaged species [29,36]. However, the net effect at the ecosystem level is more complex (Fig 2). First, resilient plant species can partially compensate for loss of sensitive species as seen in frost-drought affected dwarf shrub heathland [36], where a 55% reduction in early season Gross Primary Productivity (GPP) was followed by the absence of an effect later in the season. This apparent recovery of GPP was possibly the result of compensation by undamaged herbaceous species able to increase photosynthesis aided by a reduction in shade from the damaged shrub canopy. Similar compensation was also evident in eddy covariance flux data from a peatland in northern Norway, where an extreme winter warming event reduced GPP by at most only 12% [37].

In contrast to winter events, growing season browning events have few records and the response is often small (Fig 2). In one documented heatwave-drought event at Utqiagvik, Alaska [61] desiccation of *Sphagnum* moss was observed, but despite the *Sphagnum* CO_2 sink being reduced, Net Ecosystem Exchange (NEE) was not significantly affected (Table 1). This

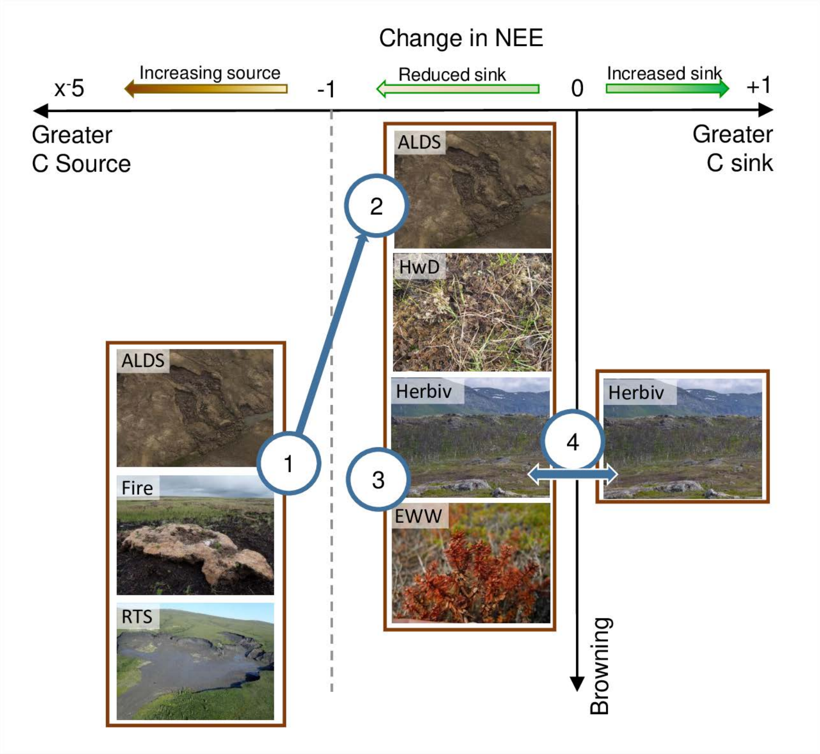

Fig 2. Browning event impacts on ecosystem carbon sequestration in the first years immediately following the event. Change in Net Ecosystem Exchange (NEE): +1 means a doubling of the pre-event (undisturbed) C uptake flux. 0 is no change with sink strength declining to −1 where there is no net uptake, x−5 means a shift to C fluxes opposite in sign (i.e., losses) but up to five-fold greater magnitude than the original C uptake flux. (1) Browning events arising from physical disturbance can result in NEE much greater in magnitude and opposite in sign than of the pre-event healthy vegetation (i.e., a shift from a C sink to a much larger C source). However, these disturbance events where there is less browning (2) can also cause more modest shifts resulting in reduced C sink size rather than conversion to a source (e.g., active layer detachments where vegetation remains partially intact or where ecosystem respiration is reduced due to lack of vegetation and reduced soil organic matter content). This more moderate change in NEE is also typical for biotic and climatic events (3) that typically result in lower C sink size rather than conversion to a source. The limitation on NEE impacts of browning from climatic and biotic drivers partially arises because photosynthesis from resilient plant species compensates for loss of sensitive species. Unique among events (4) herbivore outbreaks can also result in greater C sequestration from a rapidly recovering plant community being able to take advantage of nutrient inputs from frass, potentially doubling the C uptake compared to the original undisturbed vegetation. RTS = retrogressive thaw slump; ALDS = active layer detachment slide; Herbiv = herbivore outbreak; HwD = heatwave-drought; EWW = extreme winter warming.

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was possibly due to vascular plants compensating through earlier spring activation and protection from drought due to permafrost providing a perched water Table [61]. Furthermore, while a simulated eight-day heatwave (+9°C) in the High Arctic caused significant increases in plant growth, post-heatwave stress negated these impacts [60]. Also, greater stimulation of respiration compared to photosynthesis led to a 44% reduction in the C sink during the heatwave but no difference in C sink capacity was observed post-heatwave.

Physical disturbance events. Fires can remove large proportions of aboveground biomass and the soil organic layer, with these losses increasing with fire severity [23,66,110,111] (Table 1). Survival of vegetation above ground occurs in unburned and scorched patches within the fire perimeter [66], the prevalence of which increases with lower fire severities [65,112].

Fire increases C losses to the atmosphere substantially during the fire, but also by turning tundra ecosystems into net sources in the following years [113,114] (Fig 2). For example, 2 kg C m^{-2} was lost in the severe Anaktuvuk River fire (Alaska North Slope) from complete combustion of plant material and 19% of the soil organic matter [23] (Table 1). In the year post-fire, moderate and severe burned sites became growing season C sources of 38 and 110 g C m^{-2} summer^{-1}, respectively, in contrast to unburned sites with a net summertime sink of 44 g C m^{-2} summer^{-1} [113] (Table 1). Similar magnitude shifts were also observed in an experimental fire on a Greenland heathland [115]. Decades post fire, greater vegetation cover (greenness) suggests a larger C sink than pre-fire (see also "recovery" section below), but given vast quantities of C released in contrast with slow tundra C sequestration, a long-term increase in fire frequency and severity will likely shift tundra from a net C sink to a source at regional and larger scales [13,116].

Permafrost thaw events such as active layer detachments and retrogressive thaw slumps can result in complete loss of biomass depending on the extent to which the active layer and its associated vegetation is lost (Table 1). Active layer detachments may disturb the vegetation by translocating it downslope and exposing bare soil (Fig 1L), whereas retrogressive thaw slumps can create areas of liquefied mud denuded of vegetation (Fig 1K). Such events therefore can remove all vegetation above and below ground [86,117].

Soil wasting from acute permafrost thaw can reduce the soil C pool by 50% or more [86,118] (Table 1), potentially resulting in greater C loss than tundra fire. However, some of the transferred C may ultimately be stabilised in depositional environments so the net flux to the atmosphere may be smaller than that from fires [118]. The substantial or complete loss of vegetation in retrogressive thaw slumps and active layer detachments inevitably leads to reduced primary productivity (Fig 2). For example, retrogressive thaw slumps in High Arctic Canada have shown a range from 'lesser' responses of 75% reduction in sink capacity, to conversion to a source of 4-fold greater magnitude than the prior C sink [119] (Table 1) (Fig 2). Ecosystem and soil respiration can also be reduced due to lack of vegetation and reduced soil organic matter content, thus in some cases NEE may remain similar to undisturbed vegetation [85,86,120] (Fig 2). Nevertheless, impacts are often great, and recent work suggests active hillslope erosional features (thaw slumps, active layer detachments, gullies) could be responsible for a net release of tens of PgC by 2100 under RCP8.5 [11].

Biotic events. A year after a vole and lemming peak in sub-Arctic Sweden it was found that tundra plant biomass was between 12 and 24% lower (Table 1) [92]. In West Greenland, an outbreak of the defoliating larvae of the moth *E. occulta* caused between 26 and 45% reductions in plant community biomass in the first and second year of outbreak [99] and similar levels of browning was caused where an outbreak of geometrid moth caterpillars *E. autumnata* and *O. brumata* on birch woodland spread to tundra [121,122]. In sub-Arctic tundra, outbreak of the parasitic fungus *A. empetri* induced by experimentally increased snow cover, caused shoot mortality resulting in a more than 70% reduction in cover of the dominant dwarf shrub *E. nigrum* [106], though the deciduous shrub *Betula nana* that was not infected increased cover by more than 50%.

Few studies have quantified the effect of pulse herbivory or pathogens on C fluxes, but evidence is increasing [106,123,124] (Fig 2). In sub-Arctic tundra, an outbreak of the parasitic fungus *A. empetri* on the dominant dwarf shrub *Empetrum nigrum* caused a more than 50% reduction in instantaneous peak season GPP [106], while a larval outbreak of the noctuid moth *E. occulta* in West Greenland resulted in almost zero C sink strength in the growing season [125], and converted an average annual C sink of −30 g C m^{-2} to a source of 41 g C m^{-2} [126]. Similarly, a lemming grazing experiment (caged lemming grazing) on wet sedge tundra in Utqiaġvik, Alaska, simulating high density grazing resulted in full loss of C sink capacity [124]. In contrast, where an *E. autumnata* caterpillar outbreak spread from birch woodland into heathland, the ecosystem was unexpectedly changed from a source of CO_2 to a sink [121] (Fig 2). The mechanism is not clear but possibly plants gained advantage from the nutrient input from frass, or the reduced shading of non-vascular plants allowed for greater photosynthesis. Other biotic events have shown similar compensatory mechanisms, for instance in the case of an *E. autumnata/ O. brumata* moth caterpillar outbreak, compensation occurred through increased cover in the dominant bryophyte species, *Pleurozium schreberi* and *Polytrichum commune*. For beaver disturbance, a doubling of DOC arising from Eurasian beaver (*Castor fiber*) dam ponds indicates greater C storage, though methane emissions were also increased 15-fold compared to undammed streams [127].

Recovery and long-term changes: relatively rapid recovery for some events and potential to contribute to greening

Climatic events. Impacts of extreme climatic events on biomass and productivity appear to be largely temporary (Table 1; Fig 3). For example, following an extreme winter warming event in north-west Scandinavia (26% reduction in NDVI over 1425 km^2 [24]), NDVI recovered in two to three years, largely due to substantial resprouting from existing biomass [128]. In addition, rapid recovery even within one growing season may arise from recovery of photosynthetic capacity of physiologically stressed, but not killed, shoots [36,121]. Rapid recovery was also seen in Alaskan wet sedge tundra in response to a combined heatwave and drought, where substantial reductions in GPP recovered to pre-event levels in the second year following the event [61].

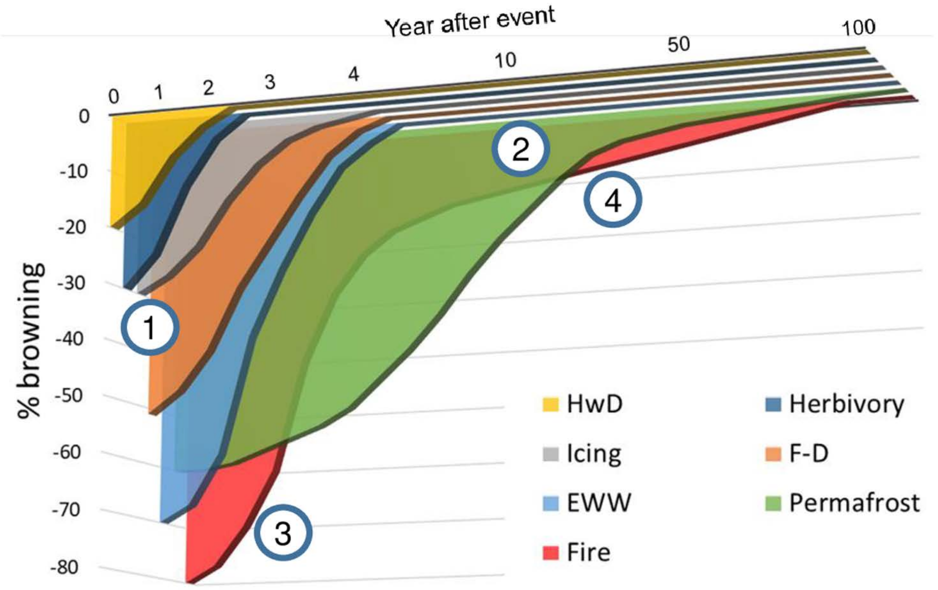

Fig 3. Overview of recovery rates of browning events. Recovery is in years since event. % browning is % loss of live biomass. HwD is heatwave-drought, EWW is extreme winter warming, F-D is frost drought. (1) Climatic events and herbivore outbreaks all have similarly fast recovery with the majority of live biomass recovered within 4 years. (2) Much longer recovery times are associated with physical disturbance events (abrupt permafrost thaw and fire), and while significant initial recovery after fire can occur on similar timescales to climatic events from re-sprouting plants, (3) full recovery can take decades. (4) Abrupt permafrost thaw has the longest recovery time due to recovery potential being severely reduced where plant biomass is completely removed above and below ground. Events may also lead to greening in the long term. % browning and recovery rates vary within a single event type, so for each event type the graph represents a 'typical' trajectory based on data and text descriptions in the cited papers.

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However, interspecific differences in sensitivity can mean some species recover more rapidly than others, signalling potential for community change and hence not recovery in terms of community composition. The observation that evergreen dwarf shrubs are more severely affected by extreme winter warming, frost drought, and icing compared to deciduous shrubs indicates that a greater deciduousness could arise from repeated events, analogous to increases in deciduousness of boreal forests arising from greater fire frequency [129,130]. This could facilitate Arctic greening through deciduous shrubification [78,131]. Furthermore, recovery of biomass may also be partially facilitated by subordinate species including greater tolerance of bryophytes and lichens, which may further benefit from the opening of the damaged shrub canopy [121] (though see [128]). Consequently, climatic extreme events (pulse disturbances) might benefit these groups in contrast to the impacts of gradual climate warming (press disturbance) [132]. Overall, while recovery from extreme climatic events appears relatively rapid (<5 yrs) in terms of biomass and productivity (Fig 3), impacts on community composition and consequences for ecosystem function may last longer or be permanent.

Physical disturbance events. Despite the capacity for fire to remove much or all aboveground biomass, scorched living tussocks of, for example *Eriophorum vaginatum*, can remain, which subsequently can exhibit abundant resprouting following the fire [65,110]. In tussock tundra therefore, initial recovery can be relatively rapid (e.g., within two to five years) (Table 1; Fig 3), at least in terms of community-level measurements such as greenness and GPP [113,133]. In contrast, lichen and moss recovery is slow, especially where much of this is removed in severe fire and may not even recover 25 years post fire [110,112]. Overall, with the rapid resprouting of tussocks, initial fire recovery can be fast, but full recovery can take decades with greater potential for longer-term legacy effects on community composition (Fig 3).

Shrub tundra recovery after fire is typically slower than recovery of tussock tundra, with initial recovery in the form of sprouting from below-ground parts by sedges and woody shrubs, and then from seed [65,110,134]. Rapid recovery of shrubs is sometimes observed within 2–3 years [133], and over 25 years shrub tundra can achieve greater biomass than pre-fire [112,135]. This suggests a longer-term potential for a more intense tundra fire regime to contribute to a greening Arctic through shrubification.

Re-establishment of vegetation after permafrost thaw events, such as retrogressive thaw slumps and active layer detachments, can be slow (Table 1; Fig 3). The first 20 years after stabilisation, vegetation can be dominated by graminoids and bare ground, with recovery of forb, dwarf shrub, and bryophyte species occurring on time-scales of decades to even hundreds of years [117,118,136]. Interestingly though, retrogressive thaw slumps can be good sites for seedling recruitment due to warmer soils, greater nitrogen availability, and less plant cover [118,134]. In such cases, vegetation recovery can be faster, with tall deciduous shrubs in Low Arctic tundra found ~10 years post disturbance [134,137]. Shrub expansion can be promoted by permafrost disturbances and so are another example of where browning events can lead to Arctic greening on decadal timescales.

Biotic events. Biotic browning events like vole and lemming peaks and moth outbreaks are regularly occurring events from which plants are well adapted to recover [92,99,124,138]. For instance, in a lemming grazing experiment on wet sedge tundra in Alaska, the 16% reduction in NDVI and loss of C sink capacity in the grazing year was no longer detectable in the subsequent year [124] and NDVI has been found to be higher due to the removal of standing dead leaf matter by herbivores the previous year [139,140]. Similarly, recovery from invertebrate herbivore outbreaks may be relatively rapid, within one or two years. For example, the substantial reduction in C drawdown caused by an outbreak of *E. occulta* in West-Greenland was immediately counteracted in subsequent years by increased productivity exceeding that of pre-outbreak years, presumably driven by increased nutrient cycling [125].

Consistent with this, ring-width analysis of grey willow (*Salix glauca*) growth following *E. occulta* outbreaks indicate reduced growth only in the outbreak year and enhanced growth in the two years after [141]. Recovery of productivity or biomass to greater than pre-outbreak levels has also been observed in other outbreaks of *E. occulta* [99], and also of *E. autumnata* and *O. brumata* [122]. As with other types of events, the caveat remains that such 'recovery' is generally described in terms of biomass and productivity, and does not necessarily mean that there are no changes in community structure [142,143].

Recovery: resistance, resilience and state shifts. Ecological principles indicate that ecosystems of long-lived, slow-growing perennials should be those with greater resistance but poorer resilience to extreme events, compared to faster-growing communities of shorter-lived species [144,145], hence Arctic ecosystems could be expected to have a high resistance but low resilience [146]. Instead, from the above evidence impacts of browning events can be substantial in magnitude (low resistance), yet recovery can often be relatively rapid (high resilience) at least to climatic and biotic events. However, recovery as measured by greenness and NEE may not capture ongoing effects on community composition, species diversity, and/or ecosystem C storage; the long-term equivalence of an unaffected ecosystem and that which has recovered its greenness following a browning event remains uncertain. Furthermore, greening may also need to be taken into account when considering recovery rates, with work indicating that recovery takes twice as long if the target recovery state is that which the ecosystem would have achieved if not disturbed (e.g., a greener ecosystem), rather than its state at the point of disturbance [147].

None-the-less, regarding biomass and productivity, climatic and biotic browning events tend to have short-term impacts, with the longer-lived impacts being more driven by physical disturbance events such as fire and rapid permafrost thaw. Similarly, browning events can be seen as causing state shifts to new stable states in line with extreme event ecological theory, for instance where they lead to shrubification, [18]. Such development of new stable states from a browning event may also be seen as an example of a 'tensioned landscape' [148] where an ecosystem resisting change from press climate change (and so under tension with the new climate) is suddenly released by the pulse disturbance allowing establishment of a plant community less in tension with (more suited to) the new climate.

Commonalities and contrasts among different event types

The pulse disturbance causes of browning events are numerous and contrast greatly with a number of different climatic, biotic, and physical disturbances. Nonetheless, several important common features emerge among the browning events they cause.

Contrasting pulse disturbances cause major loss of live biomass. All events can cause high levels of biomass loss, whether climatic (e.g., extreme winter warming), biotic (e.g., herbivore outbreak), or abiotic disturbance (e.g., fire or thermal erosion). While there is something of a circular argument here in that live biomass loss is required for a "browning" event, it is notable that many types of browning events can cause substantial biomass loss, approaching 100% of the dominant species. This finding raises the possibility of using emergent generalities to project future impacts of events on ecosystem structure and function [34,149]. However, compared to climatic and biotic events, fires have greater potential to shift ecosystems from C sinks to sources, in addition to the very substantial loss of C directly from the fire. Climatic and biotic events (despite the substantial damage) often cause reductions in C sink capacity, but do not lead to the ecosystems becoming major sources of C (due to compensation from other species, including tolerant mosses and lichens) [34,36].

Ecosystems recover relatively rapidly from many event types. Ecosystems recover relatively rapidly from many browning events, often within two to five years, though recovery is slower for severer fires and thermal erosion events, where removal of all vegetation and/or soil wasting remove or reduce the potential for belowground re-sprouting. A key factor in the recovery is that Arctic vegetation typically consists of long-lived perennials with substantial belowground biomass and re-sprouting potential, allowing recovery even when the majority of aboveground biomass is removed or killed. Overall, the capacity for recovery currently ensures that many pulse disturbances do not result in permanent, long-term browning. Future recovery may even be facilitated as warmer and longer growing seasons allow for greater growth. There are two main caveats: (i) The use of the term "rapid recovery" is in the context of slow growing Arctic plants with short growing seasons, hence with little time for recovery in any one year. We therefore consider use of "rapid" here as fair since recovery in three years of an Arctic ecosystem may represent the same amount of growing time and recovery in one year for a temperate ecosystem. (ii) Often recovery is in terms of whole-community scale parameters such as biomass or productivity, but other characteristics, such as community composition, may not recover rapidly or may be permanent.

Compensatory mechanisms reduce the negative impact on ecosystem productivity. Despite high rates of shoot mortality and loss of photosynthetic leaf area, compensatory mechanisms partially mitigate the pulse disturbance impact so that overall impacts on ecosystem carbon sequestration are smaller than may be expected from the large extent of damage. This has been most apparent in climatic and defoliating biotic events, where damage to vascular plants results in reduced shading to the ground layer, and hence allowing greater productivity of mosses, lichens or subordinate vascular plants [36,37,122]. This does though, rely on compensatory biomass being present that is tolerant of the event (e.g., especially moss and lichen cover). Where these are removed (e.g., severe fires, thermal erosion events from abrupt permafrost thaw) such mechanisms are not possible.

Browning events can lead to greening. Counterintuitively, browning events can lead to greening in the longer term. This is often seen in the form of shrubification which is a major mechanism for Arctic greening. Some browning events (e.g., fire, active layer detachments, etc.) may open up space for new establishment, which may then be colonized by plants that are more indicative of the current warmer climate (e.g., tall shrubs) [150,151]. Greater sensitivity to climatic events of evergreen shrubs compared to deciduous shrubs could lead to greater deciduousness. Beavers increase water area, but disturbances also increase exposure of mineral substrate that may facilitate shrub expansion [101].

Contrasting sensitivity between vascular and non-vascular plants. Shrubs are more sensitive to climatic events compared to bryophytes and lichens that show moderate to high tolerance. Shrubs and graminoids are also more sensitive to biotic events than bryophytes and lichens. Shrubs and graminoids may also show greater sensitivity in low-severity fires that do not remove the bryophyte or lichen layer. For high-severity fires though, bryophytes and lichens are sensitive due to being burned and having poor capacity for post-fire re-establishment. The considerable disturbance from abrupt permafrost thaw events impacts all plant groups considerably. In terms of recovery, the faster re-establishment of vascular plants compared to bryophytes and lichens where there has been major loss of most or all plant biomass again indicates contrasting sensitivity between plant functional groups.

Contrasts and commonalities, in summary. Overall, climatic and biotic events tend to be those that most often share commonalities, while key contrasts tend to arise from physical disturbance events. A look at the mechanisms and impacts of browning events suggests that this generalisation may arise because both climatic and biotic events tend to cause loss of live foliage while not necessarily killing all shoots (allowing re-sprouting) and leaving some species (especially bryophytes and lichens) relatively unharmed. In contrast, physical disturbance events may cause removal of much of the plant community, leaving less possibility for rapid recovery (re-sprouting) and fewer unharmed species to provide compensatory mechanisms.

Perspectives and future challenges

While most browning events are either known or expected to be increasing in frequency due to ongoing climate change (Table 1), it remains unclear which events will be the most important for driving browning in the future. Here it is helpful to categorize events in terms of their size and spatial distribution. Some browning events are widespread and numerous throughout many regions of the Arctic; this especially applies to fire and abrupt permafrost thaw events [11,13]. While the spatial extent of individual permafrost thaw events may often be small when compared with other events considered here, their relatively frequent occurrence and wide distribution indicate that they will remain among the primary drivers of browning events at the pan-Arctic scale. Fires can affect a larger area with a single occurrence, and also occur over a large spatial domain. These factors, combined with their increasing frequency, suggest fires may also become the most important pan-Arctic driver of browning. Climatic and biotic events fit a category that can be described as often large in size (for an individual event), but either less common throughout the Arctic (biotic events) or common but currently restricted to some regions (as far as the evidence suggests, e.g., extreme winter warming). These events may be the main drivers of Arctic browning in particular regions but have no importance in others. Such regionally-limited events may spread as the Arctic continues to warm, but work is needed here to establish projections with confidence.

At least for permafrost and fire, there are strong and coordinated efforts addressing uncertainties (e.g., [11,26,13,69]). In contrast, efforts to predict future changes in frequency and extent of climatic and biotic events are at an earlier stage, and currently there is a need for greater links between studies projecting these pulse disturbances and the resulting browning that can arise. Furthermore, pulse disturbances can interact (see [7]), for instance dead, dry, plant material from drought may promote fire, or fire may promote conditions for permafrost thaw. However, given most work focusses on one browning event type, more work is needed to understand the impacts of a future of interacting disturbances.

Predicting the frequency and understanding the impacts of future browning events will be challenging [5,149]. These events are generally hard to study, occur abruptly and are difficult to predict; so being on site to study them in progress is difficult, especially in the vast expanse of the Arctic, where logistics pose an additional challenge to observations. Arctic research broadly should have much improved and genuine collaboration with Indigenous people and other Arctic residents from the onset, and the challenges posed in studying browning events will be better addressed with such an approach [152,153]. Furthermore, while remote sensing provides a powerful tool for studying browning events, there can be a disconnect between what is observed remotely and what is observed on the ground [6,9,154]. Additionally, the remotely-sensed signals of some browning events can be very similar (e.g., the damage resulting from frost drought, icing, and extreme winter warming), preventing attribution to a single causal mechanism, unless there are supporting ground observations or fine-scale meteorological data.

To better address the challenges of understanding the future consequences of browning events in the Arctic, we propose the following priorities:

(1) ***Characterise the baseline conditions*** - i.e., how frequent were browning events in the past, and what is their current frequency and extent geographically? This will ensure we can better understand how browning events have naturally influenced Arctic ecosystems, and therefore better understand the possible impacts of increases in frequency. Here historical remote sensing data can be used to link to known past browning events. When linked with climate data, greater understanding of the causes of browning can also be achieved [155]. People that live in areas of browning events are an important source of knowledge on historic frequency (see also point 6, collaboration with indigenous and local communities).

(2) ***Quantify the links between pulse disturbances (extreme events) and press climate change***, and therefore improve predictions of how browning event frequency or intensity will change. For some types of browning events, evidence and understanding is focussed in one or a few regions. There are large areas of the Arctic where it remains unclear which, if any, browning events occur on the ground (to "western" scientists at least, see point 6), and this restricts our ability to project event importance and spread in the future. Data to address this will need more sampling and observations in regions with low representation. Collection of this data can work best when done in standardized ways across locations (for example, the CAFF's extreme event monitoring tool provides a helpful solution [156]). Better understanding of the climate/weather conditions that cause pulse browning events will facilitate modelling of future frequencies and intensities in a changing climate. This can be better informed also from greater understanding of the past base-line (point 1), and also with more experimental efforts, both outdoors (field experiments) and in climate-controlled chambers (see also point 3).

(3) ***Examine how impacts of browning vary among vegetation types, plant functional types, populations, and life stages***. The level of knowledge varies greatly among types of browning events. The issue of knowledge sometimes being limited to only some Arctic regions (point 2 above) also applies here, meaning that we do not know the consequences for all vegetation types in which browning events may occur. Collecting data from events when they occur provides an opportunity, because many events are at a scale that allows assessment of a number of different plant communities. Such work, should include more data on biodiversity-ecosystem structure responses because to date there has tended to be a greater focus on plant mortality and biomass loss, with less on compositional change. For data on responses at the level of species, functional types and life stages, growth chamber and experimental plot studies can be useful due to the large number of different species that can be included [157]. The experimental control possible in these more reductionist approaches can also provide data on what the thresholds are for different species to result in the mortality that creates the browning (especially for climatic events, e.g., how long do warm temperatures need to last to initiate premature bud burst in extreme winter warming events).

(4) ***Test how browning affects the biogeochemical and biophysical feedbacks to climate.*** For many browning event types (especially climatic and biotic), biophysical feedbacks have been little studied, hindering our ability to incorporate these into Earth System Models. Understanding is better for fire and permafrost thaw, but all event types need more data. Addressing this data need could include more space-for-time studies, targeting specific neighbouring sites with and without recent browning events, and with data focussed on comparing specific biophysical feedbacks (e.g., changes in evapotranspiration, albedo, carbon loss). Data can be drawn from remote sensing and field-based instruments, depending on the needed resolution, accuracy and precision. For biogeochemical cycling, much more data is needed on below ground responses (especially for climatic and biotic events), given we should expect significant impacts on microbial communities and biogeochemical cycling resulting from the abrupt cut-off of C supply from plants, and impacts on ground temperature (loss of shading) and moisture (loss of plant transpiration). For many events, more data is also needed on the consequences for nutrient availability especially as this could impact recovery rates [158].

(5) ***Improve the inclusion of browning in models.*** This work should include bottom-up approaches, where environmental variables with quantifiable causal influence over the occurrence, rate and biogeochemical consequences are identified (e.g., [159]), with a focus

on environmental variables that can be quantified across heterogeneous Arctic regions [149]. Data on bottom up controls include information on plant species identity both geographically (what species are where particular events occur, and their response and sensitivity in terms of thresholds that cause mortality), and topo-graphic controls that modify response. More data is needed on top-down climatic controls that create the conditions for the browning event (see points 2 and 3).

(6) ***Collaboration and reciprocal knowledge sharing with Indigenous communities in browning research.*** Browning events can have direct consequences for Indigenous peoples of the Arctic through impacts on local infrastructure and natural resources. Acknowledging the collective benefit for including Indigenous perspectives, research should adopt recommendations for co-production with Indigenous peoples for improved recording, prediction and adaptation [153]. Such work should include Indigenous knowledge holders from the outset to inform research design, should promote Indigenous governance and self-determination in research, and leave a legacy of capacity building and training [160,161]. Use of standardised protocols for data collections (point 2) can apply here, but also Indigenous knowledge holders have a wealth of insight into occurrence of extreme events. Through reciprocal knowledge sharing, better understanding of which events are most impactful to livelihoods and resources should also be used to help set priorities for future research.

Conclusions

The pulse disturbances that cause Arctic browning events are numerous and diverse, which presents challenges in understanding current and future browning and its consequences. First, we identified a suite of pulse disturbances that cause browning events that are most frequently observed with the greatest impacts (fire, abrupt permafrost thaw, extreme winter climatic events, invertebrate herbivore outbreaks). Data, modelling, or extrapolations from climate change projections indicate many pulse disturbances that cause browning are either already increasing or are likely to increase in the future. Second, we found that Arctic ecosystems show capacity for relatively rapid recovery from many browning events especially where only certain plant functional types are impacted and live biomass is left for re-growth. Third, we identified that for many (though not all) events, impacts on C sequestration can be lessened by compensatory mechanisms. In the longer term, evidence suggests that browning events can lead to greater biomass production, and - ultimately - become drivers of Arctic greening. Fourth, we identified six research priorities based on perceived knowledge gaps.

Given that many types of browning events are already increasing in frequency, greater understanding is needed if we are to adequately predict the future for Arctic terrestrial ecosystems, consequences for biodiversity, feedbacks to climate, and ultimately the consequences for Arctic societies that rely on these landscapes.

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